6. On the Structure of the Reptilian Tarsus.

By R. Broom, D.Sc., F.R.S., C.M.Z.S.

[Received November 9, 1920: Read February 22, 1921.]

(Text-figures 1–27.)

In 1864 Gegenbaur established the general homology of the elements of the tarsus with those of the carpus, and gave us a series of names for the elements which have been used by most later writers.

The typical carpus in the higher forms was shown to be made up of a radiale and an ulnare with an intermedium between them, a centrale near the middle of the carpus, and five distal carpalia. In the hind limb the tibia and fibula undoubtedly correspond with the radius and ulna of the fore limb and the five distal tarsalia as unquestionably agree with the five distal carpalia, but as the proximal part of the tarsus usually has only three elements, there has always remained some little doubt as to how to homologise them with the four proximal carpals.

Gegenbaur considered that the two proximal elements of the mammalian tarsus—the calcaneum and astragalus—corresponded with the ulnare, the intermedium, and radiale of the fore limb, and that they ought to be regarded as the fibulare and conjoined intermedium and tibiale, while the third element, the navicular, he looked upon as the centrale of the tarsus. As the intermedium and radiale are frequently united in mammals, it seems very natural to conclude that the intermedium might be permanently fused with the tibiale in the tarsus.

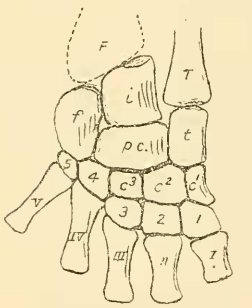
Gegenbaur's view has been followed by the majority of later comparative anatomists and palæontologists. When it was seen, however, that there was no evidence from either palæontology or from the study of the skeletogenesis in favour of the astragalus being a composite element, most workers came to favour the view that the astragalus is the tibiale alone and that the intermedium has been early lost, though some few preferred to look on the astragalus as the intermedium and to consider that it was the tibiale that was lost. At the present time, though the large majority of authorities support the former view, the question is by no means settled, and I think there are good reasons to believe that the generally accepted view is a mistaken one. Within recent years, palæontology has given us so much new light that it seems necessary to reopen the question.

If we had well-preserved tarsi of all the Carboniferous and Permian amphibians and reptiles known, there would be no difficulty in giving the complete evolutionary history of the tarsus in its later stages. Unfortunately, the tarsus of most of the early Tetrapods remained largely cartilaginous, and even where the elements are ossified it is rarely that we find them in

undisturbed positions. Still, we have a few early tarsi sufficently well preserved to suggest to us the main lines of evolution.

The most primitive Tetrapod tarsus known is that of the Temnospondylous amphibian, *Trematops milleri* Williston, from the Lower Permian Beds of North America (text-fig. 1). Here we find the tarsus composed of four large proximal elements, one of which is situated centrally, five distal tarsalia and three centralia lying above the first, second, and third tarsalia. The element articulating with the end of the tibia we ought, I think, to call the tibiale, even though it is not, as I hope to show, the same element as articulates with the tibia in the higher forms. The other two proximal elements must be regarded as the fibulare and the intermedium. These determinations are those of Williston, and it is difficult to see how they can be disputed. Williston points out that there has been a passage for vessels between the fibulare and the intermedium.

Text-figure 1.



Text-figure 2.

Text-fig. 1.—Right tarsus and metatarsus of *Trematops milleri* Williston *, slightly modified after Williston.

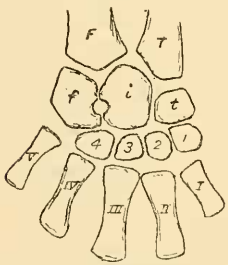
Text-fig. 2.—Right tarsus and metatarsus of *Uranocentrodon senekalensis* v. Hoepen †. The tarsal elements are figured in true relative position, as seen in two different specimens. Letters indicate the probable position of the elements which have remained cartilaginous.

* An American Lower Permian Temnospondylous Amphibian.
† A South-African Upper Permian Temnospondylous Amphibian.

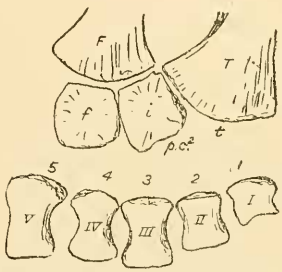
Our South African Upper Permian Temnospondylous form, *Uranocentrodon senekalensis* v. Hoepen (text-fig. 2), gives us a further development of the amphibian tarsus. Though the tarsus is here imperfectly ossified, we have two specimens with the elements in almost undisturbed relations, so that we can be fairly sure of their determinations. As will be seen from the figure I give, there are three large, proximal, well-ossified elements and three imperfect ossified distal elements. If we had not the clue afforded by *Trematops*, we might determine the proximal elements as the fibulare, intermedium, and tibiale. We might perhaps, even

more readily regard them as the fibulare, tibiale, and centrale from their superficial resemblance to the calcaneum, astragalus, and navicular of the mammalian tarsus. It is, however, quite manifest that, whatever the tibia supports, it is not the element lying on the tibial side of the fibulare. We can readily see that this element is the one which we have identified as the intermedium in *Trematops*. It is similarly situated, and it has between it and the fibulare a passage for vessels exactly as in *Trematops*. The element situated distal to this intermedium is manifestly the proximal centrale. The tibiale has remained, like the majority of the other elements of the tarsus, cartilaginous. The other ossified elements of the tarsus are figured as they occur. I identified them as the first and fourth distal tarsals and one of the centrales. Haughton, in describing the tarsus in the Bloemfontein specimen, regards the distal elements as the first and third, but the Pretoria specimen has the element in undisturbed

Text-figure 3.



Text-figure 4.



Text-fig. 3.—Right tarsus and metatarsus of *Scincosaurus crassus* Fritsch *. After Jaekel.

Text-fig. 4.—Right tarsus and metatarsus of *Limnoscelis paludis* Williston †. The positions of the missing elements, which were probably cartilaginous, are indicated by letters.

* A Microsaurian amphibian.
† A primitive Cotylosaurian reptile.

articulation with the head of the fourth metatarsal. Haughton agrees in regarding the third small ossification as the centrale. When the cartilaginous elements are restored, it will be seen that the tarsus is almost exactly similar to that of *Trematops*.

The most interesting feature of the *Uranocentrodon* tarsus is the tendency that it exhibits of the elements on the tibial side to become reduced.

The next tarsus which we are able to study is that of the Microsaurian *Scincosaurus crassus* Fritsch. (text-fig. 3). Whether the Microsauria are to be regarded as reptile-like amphibians or as amphibian-like reptiles need not at present concern us, as it is agreed by most that if they are amphibians they are apparently the nearest to the primitive reptiles. It is extremely fortunate

that we have this tarsus well preserved, as it shows us how the reptilian tarsus has been derived from the primitive amphibian type. As figured by Jaekel, it has three proximal elements and four distal. The elements articulating with the fibula are manifestly those we have identified in the more primitive type as fibulare and intermedium, and they are so identified by Jaekel. The third proximal element articulates with the tibia and is manifestly the tibiale. It is much smaller than the other proximal elements. The distal elements are the first four distal tarsalia. Between the fibulare and the intermedium is the tarsal foramen.

The great difference between the Microsaurian tarsus and that of the Temnospondylous types is that in the former all the central elements have disappeared or become generally reduced and cartilaginous.

In the earliest undoubted reptiles known—the Cotylosauria—the tarsus has only been preserved for us in a very few forms.

In *Limnoscelis paludis* Williston (text-fig. 4), though the tarsus is not perfectly preserved and was probably largely cartilaginous, we have the two principal elements preserved in position. Williston identifies them as the fibulare and the united tibiale and intermedium, but it seems much more probable that they are the fibulare and the intermedium, and that the tibiale is either lost or was cartilaginous, and this latter view is admitted by Williston as not impossible.

Another very primitive type of which we know the tarsus is *Eosauravus copei* Williston (text-fig. 5), from the Middle Pennsylvanian of North America. Unfortunately, the head of this animal is unknown, and we are thus in doubt whether or not it is a Cotylosaur. The tarsus has the elements preserved in only slightly disturbed relations. There are two large proximal elements, which a comparison with other early types leads us to consider as the fibulare and intermedium. There are five distal tarsals, and a small element on the tibial side of the tarsus which is probably the reduced tibiale. The metatarsals are somewhat displaced, and it is not improbable that the distal tarsals and the tibiale are also a little displaced.

In *Seymouria baylorensis* Broili (text-fig. 6) the nearly perfect tarsus has been discovered by Williston. It consists of two large proximal elements and a third small one, and apparently five distal tarsals. The two large tarsals are regarded by Williston as the fibulare and tibiale, and the small proximal element the centrale. I interpret them as in *Scincosaurus*—the fibulare, intermedium, and tibiale.

The only other Cotylosaur in which the tarsus is satisfactorily known is *Procolophon trigoniceps* Owen (text-fig. 7), and though *Procolophon* in having a roofed temporal region is usually placed with the Cotylosaurs, yet, being a late Triassic form, it has advanced in many respects so far from the Cotylosaurs of the Permian of North America that it ought, perhaps, really to be

placed in a distinct order—the Procolophonia. The tarsus is known with the elements in undisturbed position. There are two ossified proximal elements and four distal tarsalia. The two proximal elements have a passage between them, and are manifestly the homologues of the large elements in *Scincosaurus* and thus the fibulare and intermedium. There has possibly been a cartilaginous tibiale, which is not preserved, as it seems necessary to have an element to the tibial side of the intermedium to support the first tarsale. Goodrich's figure of the *Procolophon* tarsus, which is taken from Watson's much-reduced restoration, gives rather a misleading idea of the structure. In *Procolophon* the radiale in the carpus has evidently been cartilaginous, and it is thus not at all remarkable that the corresponding tibiale in the tarsus should also remain cartilaginous.

When we follow the line of mammalian descent through the American Pelycosaurs and allied forms and through the South African Therapsids, we have as many well-preserved tarsi as we require.

Text-figure 5. Text-figure 6. Text-figure 7.

Text-fig. 5.—Right tarsus and metatarsus of *Eosauravus copei* Williston*. After Williston. The distal tarsals are evidently somewhat displaced. The large oval element between the intermedium and the first metatarsal is probably the displaced tibiale. The smaller element lying proximally to it is probably the first tarsal. The largest distal tarsal is probably the fourth tarsal.

Text-fig. 6.—Right tarsus and metatarsus of *Seymouria baylorensis* Broili †. After Williston.
The third and fourth tarsalia are lost.

Text-fig. 7.—Right tarsus and metatarsus of *Procolophon trigoniceps* Owen‡. From a specimen in the Albany Museum. The elements are preserved in almost undisturbed relations. There was most probably a small cartilaginous tibiale in the position indicated by the letter "t."

* A primitive Reptile of unknown affinity.

† A primitive Cotylosaurian reptile.

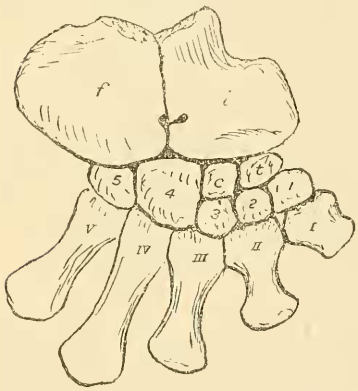
‡ A late Upper Triassic Cotylosaurian reptile

The most primitive type we know is *Ophiacodon mirus* Marsh (text-fig. 8). Here there are two large proximal elements, manifestly those which become the calcaneum and astragalus of the mammal, with five distal tarsals and two small elements lying distal to the astragalus. The calcaneum and astragalus are manifestly again the two elements which in lower types we have identified as fibulare and intermedium; and the five distal tarsals present no

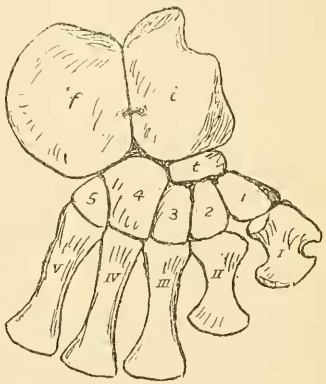
difficulties. The two elements in the centre of the tarsus, however, may readily give rise to difference of opinion. By Williston, Case, and others who have written on the type they are regarded as first and second centralia. The inner of the two is the element which becomes the mammalian navicular. The outer one is an element which becomes early lost, and is only known in a very few Permian forms.

If we identify, as I think we must do, the astragalus with the intermedium, we must either regard the tibiale as lost, or find it is the inner of the two supposed central elements. This inner element supports the first tarsal, and though it appears to have slipped away from the tibial articulation, it is still not far removed from the tibia. If we are right in identifying the inner proximal elements in *Scincosaurus* and *Seymouria* as the tibiale,

Text-figure 8.



Text-figure 9.



Text-fig. 8.—Right tarsus and metatarsus of *Ophiacodon mirus* Marsh*. After Williston. Slightly modified.

Text-fig. 9.—Right tarsus and metatarsus of *Casea broilii* Williston†. After Williston.

* An early Theromorph.

† An aberrant Theromorph.

then there is good reason to believe that the navicular of the Pelycosaurs, the Therapsids, and the Mammals is also the tibiale which by the lengthening and narrowing of the tarsus has become slightly altered in position. In the Cotylosaurs the distal tarsals are nearly twice as wide as the fibulare and the intermedium. In the more active Pelycosaurs the tarsus has become so narrowed that the distal tarsals together measure often less and rarely much more than the width of the two large proximal elements. If the tibiale is to be retained at all it can only be by becoming wedged in between the intermedium and the first and second tarsalia. This, I believe, is what has happened;

and it is remarkable, as I hope to show presently, that a similar shifting of the tibiale is also seen in Sauropsida, and perhaps it has arisen independently in this group.

In *Casea broilii* Williston (text-fig. 9) the small central element has disappeared, and we thus have a tarsus that, except for retaining the fifth tarsale, is essentially mammalian in structure.

In *Varanops brevirostris* (Williston) (text-fig. 10) the tarsus is like that of *Casea* and *Ophiacodon*, except that not only has the centrale disappeared, but the tibiale is evidently cartilaginous.

In the Therapsids the tarsus is almost typically mammalian in structure. There is never a centrale, and the tibiale is always placed, as is the navicular in the mammal, between the intermedium and the first and second tarsals.

In Anomodonts the tibiale is frequently cartilaginous either wholly or in part. Many years ago I figured the tarsus in a small form which I referred to *Udenodon gracilis* Broom. Shortly afterwards I found that the skeleton belonged to the same animal

Text-figure 10. Text-figure 11. Text-figure 12.

Text-fig. 10.—Right tarsus and metatarsus of *Varanops brevirostris* (Williston). A primitive Pelycosauroid reptile. After Williston.

Text-fig. 11.—Right tarsus and metatarsus of *Emydopsis trigoniceps* (Broom), a small Anomodont reptile. The drawing is mainly from the specimen in the Albany Museum, but partly restored from other specimens. The condition of the tibiale varies greatly in Anomodonts. In some it is completely cartilaginous, in others well ossified. It probably affords part of the articulation for the tibia.

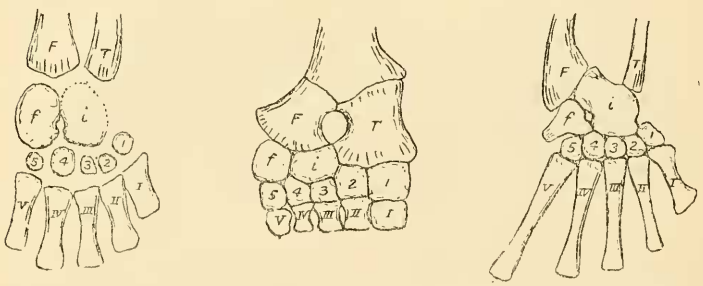
Text-fig. 12.—Right tarsus and metatarsus of *Galechirus scholtzi* Broom, a small Dromasaurian reptile. The elements are figured as found, but the intermedium is evidently slightly rotated.

as the skull which I had called *Oudenodon trigoniceps* Broom. We now know that this small Anomodont has a few small molars, and must be placed in a new genus, *Emydopsis*. I give a new figure of the tarsus (text-fig. 11). The interesting point about it is that the tibia probably articulates with the tibiale. In another small Anomodont tarsus I have belonging to an undescribed species, the tibia also appeared to articulate with the tibiale.

In the more mammal-like forms—the Gorgonopsians and the Cynodonts—the tibia and fibula articulate only with the intermedium and the fibulare.

The most primitive known tarsus of the lizard-like group is that of *Broomia perplexa* Watson. Though the top of the skull of this animal is unknown, almost all the rest of the structure is known, and fortunately the tarsus is almost perfectly preserved. As in the large majority of early reptiles, there are two large proximal elements. There are five distal tarsals and two other small elements. The two proximal elements have the usual foramen between them, and are doubtless the fibulare and intermedium. The two small elements are regarded by Watson as the first and second centralia. I regard the inner one as the imperfectly ossified tibiale. The distal end of the tibia as found is in a position to articulate with what I regard as the cartilaginous position of the tibiale. Watson, in his restoration, shifts the tibia to make it articulate with the intermedium, which he regards as the fused intermedium and tibiale. If we articulate the tibia as Watson has done, the three first digits seem practically without any proximal support—a condition which

Text-figure 13. Text-figure 14. Text-figure 15.



Text-fig. 13.—Right tarsus and metatarsus of *Palæohatteria longicaudata* Credner. A primitive Permian reptile of doubtful affinity. Regarded by Williston, Watson, and others as a Theropsidan: by the writer and others as an early Sauropsidan. After Jaekel.
A cartilaginous tibiale was probably present.

Text-fig. 14.—Right tarsus and metatarsus of *Mixosaurus nordenskjöldi* Hulke. A Triassic Ichthyosaur. After Wiman.

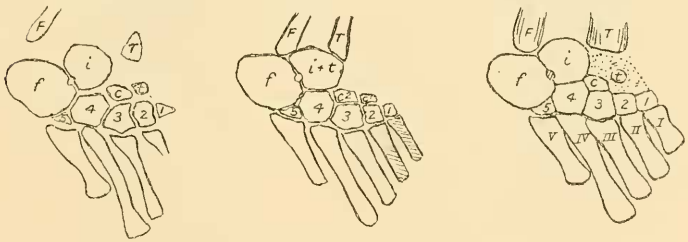
Text-fig. 15.—Right tarsus and metatarsus of *Stereosternum tumidum* Cope. A Lower Permian Mesosaurian. After M'Gregor.

seems very improbable. The second small element is doubtless, as Watson holds, a centrale. I give a figure of the tarsus as found, as restored by Watson, and as I am inclined to restore it (text-figs. 16–18).

There is another primitive reptile which one wishes one knew more about. I refer to *Palæohatteria longicaudata* Credner. Though first described over thirty years ago, and apparently known by very satisfactory and nearly complete skeletons, we are still in much doubt about the animal and its affinities. For many years it was believed by every one to be a primitive two-arched

reptile allied to *Sphenodon*. But a few years ago Williston came to the conclusion that it was a Pelycosaur or a near ally, and Watson holds a similar opinion, stating that "it now seems almost certain that *Palæohatteria* is really a Therapsid." It is difficult for one who has no chance of seeing the actual types to know which authorities he ought to follow, and though the tendency is always to follow the latest, I personally do not feel at all satisfied that Williston and Watson are right in this matter. The skull as restored by Jaekel—and his restoration seems to me the best we have yet had—is very unlike that of any Pelycosaur or Therapsid: the shoulder-girdle is entirely unlike and the pelvis is only a little like. The humerus also has only a very slight resemblance to that of a Pelycosaur or Therapsid. Fortunately the tarsus is fairly well preserved, and, as figured by Jaekel, has two large proximal elements, which he considers, as also I do, to be the fibulare and intermedium (text-fig. 13). The only other ossified elements are the five distal tarsals. Possibly there has been a cartilaginious tibiale. If so, the only difference between

Text-figure 16. Text-figure 17. Text-figure 18.



Text-fig. 16.—The right tarsus and metatarsus of *Broomia perplexa* Watson. A primitive Permian Sauropsidan. The remains as found. Left reversed. After Watson.

Text-fig. 17.—The tarsus and metatarsus of *Broomia* as restored by Watson.

Text-fig. 18.—The tarsus and metatarsus of *Broomia* as restored by the writer.

the tarsus of *Palæohatteria* and that of *Broomia* would be that the former had lost the small centrale.

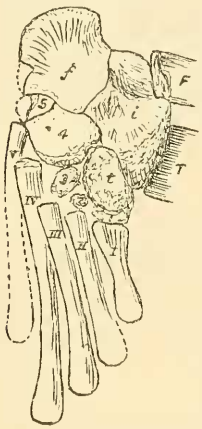
On the evidence of the published figures of *Palæohatteria* I am inclined to regard it is a primitive Diapsid reptile, a little more advanced than *Broomia* and a little more primitive than *Youngina*.

Youngina is the only known Permian Diapsid in which the tarsus is fully ossified and almost perfectly preserved (text-figs. 19 & 20). In this tarsus there are two large proximal elements—the fibulare and intermedium with the tarsal foramen between them, five distal tarsalia, and a large element situated between the intermedium and the first, second, and third tarsalia, which I believe to be the tibiale.

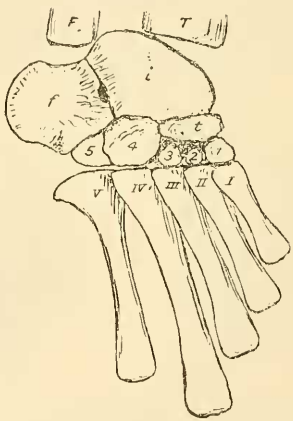
The fibulare is a flat bone which has a very distinct heel process. The intermedium is very large and with a large

articular surface for the tibia. It articulates with the fibulare, the tibiale, and the fourth tarsal. The tibiale is relatively small, and is wedged in between the intermedium and the first, second, and third tarsalia. Though the tibia does not articulate with it in most positions of the foot, it seems probable that it does when the front is turned inward, as is manifestly possible. The three first distal tarsals are all small but well ossified. The fourth is very large; its relations will be seen in the figure given. The fifth tarsal is moderately large and flat; it articulates with the fourth tarsal by a suture which allows very little movement between the two.

Text-figure 19.



Text-figure 20.



Text-fig. 19.—Left tarsus and metatarsus of *Youngina capensis* Broom *, as preserved. The foot has the plantar surface displayed, and the metatarsals are somewhat distorted. Twice nat. size.

Text-fig. 20.—Right tarsus and metatarsus of *Youngina capensis* Broom, viewed from the dorsal side, with the metatarsus restored in position. The tibiale, first, second, third, and fourth tarsals of the right side are preserved in position, and have their dorsal aspects displayed. The fibulare and part of the intermedium of the left side have had their dorsal surfaces exposed and are added to the drawing reversed.

* A Permian two-arched reptile of the order Eosuchia.

The metatarsals are long, slender, and moderately straight bones. The fifth metatarsal, which we should have expected to be of the *Sphenodon* hooked type in this undoubted two-arched reptile, is a long slender bone, nearly as long as the fourth metatarsal, and it shows no trace of the peculiar hooking. The upper end is expanded, and the outer process probably was attached to the fibulare by a ligament.

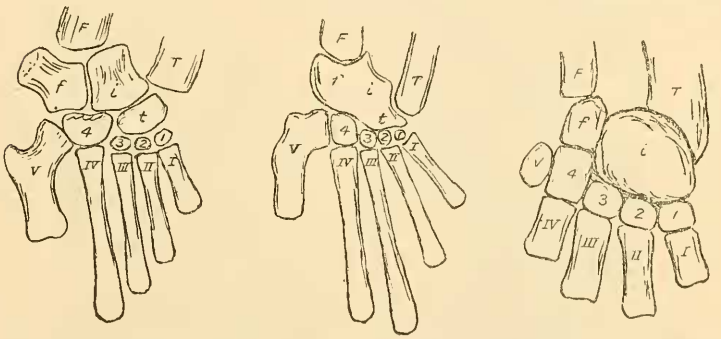
The remarkable points in the foot of *Youngina* are this primitive generalized fifth metatarsal, and the fact that the tarsus

is almost typically Therapsid or even mammal-like. A few years ago I figured a well-preserved tarsus under the name *Galesphyrus capensis*, believing it to be a Dromasaurian. The few points in which it differs from the Dromasaurians are points in which it agrees with *Youngina*, so that it is much more likely that it is an Eosuchian.

Another very interesting tarsus is that of the South African Upper Triassic Rhynchosaurian, *Howesia browni* (text-fig. 21). The tarsus is almost perfectly preserved though doubled over, and the restoration I give is probably nearly correct. There is a large fibulare with a heel process, a large intermedium, and a smaller tibiale. There are four distals, and the fifth metatarsal has the *Sphenodon*-like specialization.

The tarsus of the adult *Sphenodon* is well known, and Howes and Swinnerton have given us something of the embryonic

Text-figure 21. Text-figure 22. Text-figure 23.



Text-fig. 21.—Right tarsus and metatarsus of *Howesia browni* Broom; a Triassic Rhynchosaurian.

Text-fig. 22.—Right tarsus and metatarsus of an embryo of *Sphenodon punctatus* Gray. The embryo is of Dendy's stage R. Ossification has commenced in the metatarsals. Though the proximal tarsal cartilaginous mass shows no clear evidence of its nature at this stage, earlier embryos show that it is composed of three elements, and I think only three.

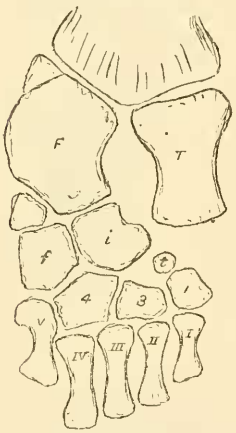
Text-fig. 23.—Right tarsus and metatarsus of an embryo of *Testudo* sp. The embryo is of the stage where chondrification is well advanced, but where ossification has scarcely begun. The very marked difference between this tarsus and that of the *Sphenodon* embryo is of interest.

condition. Only those who have studied developing cartilage and procartilage know the difficulties of this mode of research. At times we get remarkable results, but too often they are inconclusive. I give a figure (text-fig. 22) of the tarsus in a young embryo of *Sphenodon*, which I was able to examine through the kindness of Prof. Dendy. Though ossification of the metatarsals is just commencing at this stage, there is no clear evidence of the composite nature of the large proximal element. Howes and Swinnerton showed that there was evidence at an earlier stage

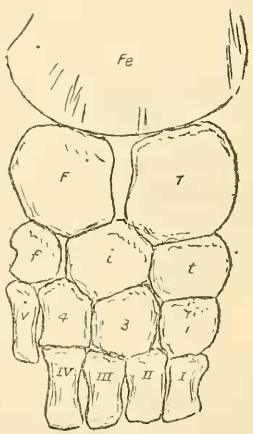
of its being made up of a fibulare, an intermedium, a tibiale, and a centrale. I think it more probable that there are only in it the fibulare, intermedium, and tibiale. The evidence for a centrale is not at all satisfactory. If, however, it is really the conjoined fibulare, intermedium, and tibiale, then the whole tarsus becomes strikingly similar to that of *Howesia*.

I give a figure of the tarsus of a very young embryo of *Testudo* sp. (text-fig. 23). Here there are only seen two proximal elements and four distal tarsals. There is no evidence of the larger proximal elements being more than a single element, and I am inclined to regard it as intermedium alone. Other Chelonians are known to have an additional element between the larger proximal element and the first and second tarsals.

Text-figure 24.



Text-figure 25.



Text-fig. 24.—Right tarsus and metatarsus of *Plesiosaurus rugosus*. After Owen.

Text-fig. 25.—Right tarsus and metatarsus of *Peloneustes philarchus* Seeley. After Andrews.

Goodrich considers this to be the centrale. I regard it as the much reduced and displaced tibiale. The fifth metatarsal is shortened up.

In most of the later Diapsidans we find a tarsus which is either of the *Sphenodon* type or a modification of it.

In the aquatic reptiles we find many interesting types. *Ichthyosaurus* is too specialized to be of much morphological interest, but the Triassic form, *Mixosaurus*, shows us how the Ichthyosaurian paddle has originated. I believe the tarsus to be made up of fibulare and intermedium with the five distal tarsals, and to be thus almost identical with the tarsus of *Mesosaurus* or *Stereosternum*, which there is some reason to consider as perhaps its nearest allies.

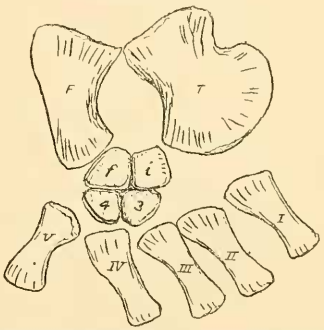
The Plesiosaurian tarsus (text-figs. 24, 25) presents little difficulty. The fibulare and intermedium are well ossified, but in the earlier forms the tibiale is often partly or wholly cartilaginous. In later types the tibiale is well developed. There are only three distals, which I believe to be first, third, and fourth. The fifth metatarsal is shortened up as in Chelonians.

The Pythonomorphs show a most interesting type of tarsus. In *Mosasaurus* (text-fig. 26) there are only three tarsal elements, which are manifestly the fibulare, the intermedium, and the fourth distal tarsal. In *Platecarpus* (text-fig. 27) there are four tarsal elements—the fibulare, intermedium, and the third and fourth distal tarsals. In both types there is a specialized fifth metatarsal.

Text-figure 26.

Text fig. 26.—Right tarsus and metatarsus of *Mosasaurus lemonnieri* Dollo. A European Pythonomorph. After Dollo.

Text-figure 27.



Text-fig. 27.—Right tarsus and metatarsus of *Platecarpus abruptus* Marsh. An American Pythonomorph. After Williston.

In the reptilian and amphibian tarsus the most remarkable features are the almost constant presence of the fibulare and the intermedium, and the great variability of the tibiale. Rarely is the tibiale a large element: very frequently it remains entirely or partly cartilaginous. In many types it is completely absent. In the mammal-like reptiles and in the primitive Diapsidans it is wedged in between the intermedium and the first and second tarsalia.

The central elements, of which there are four in some amphibians, are early greatly reduced and lost. The only one which for a time remains in early reptiles is apparently the homologue of the proximal centrale in *Trematops*. In only a few Permian forms is it still present, and in no Triassic or later reptile is there any trace of it.